POPULATION ANALYSIS AND ORIENTATION STUDIES OF GRAPTOLOIDS FROM THE MIDDLE ORDOVICIAN UTICA SHALE, QUEBEC

by SUSAN RIGBY

ABSTRACT. Three large populations of graptoloids from the Middle Ordovician Utica Shale of Quebec contain *Orthograptus quadrimucronatus micracanthus* and *Amplexograptus praetypicalis*. Detailed orientation studies show that the two species reached the bedding plane at different times and were probably present in the water mass as monospecific shoals. Some size ranges of each population are orientated, suggesting that current sorting occurred. Few siculae are present, either because of current winnowing or because of geographical separation of growth stages in life. Length–frequency graphs of complete specimens suggest that both species grew throughout life. Survivorship analysis indicates that some populations died from constant environmental stress while others lived long enough for increasing length (or age) to become a handicap. The origin of synrhabdosomes is considered to be taphonomic.

ALTHOUGH graptoloids are often very abundant when they are found, few studies of such populations have been undertaken. A notable exception is the work of Cisne and Chandlee (1982), who analysed a large number of specimens collected from a transect across late Middle Ordovician sediments in the Mohawk Valley, New York, USA. This transect included the Utica Shale and its shallow water equivalents. The graptoloids were identified at the generic level and analysed for relative and absolute abundances to elicit environmental information. The graptoloid samples were collected over 1 m thick packets of rock, each representing approximately 50000 years of deposition.

The present study is a pilot attempt to investigate the information-carrying potential of individual graptoloid populations preserved on single bedding planes and which presumably lived and died over a short period of time.

GEOLOGICAL SETTING

The Utica Shale, deposited during the late Middle Ordovician (Riva 1969), was interpreted (Bradley 1989) as having been laid down in deep water within a small and closing ocean basin. This basin was situated between mainland Laurentia and the approaching Taconic island arc. Collision occurred later in the Quebec area than to either north or south. This was attributed to a local but deep embayment of the coastline. The enclosed Taconic Ocean probably had a width of 500–900 km at its fullest development.

In the Neuville area of Quebec, Canada, the Utica Shale is well exposed on the shores of the St Lawrence River and in roadside cuttings and cliffs. It contains abundant and well-preserved graptoloids. The fauna is otherwise sparse, but includes coiled gastropods, small brachiopods and orthocone nautiloids. From this low diversity and preponderance of planktonic organisms, and from the high carbon content of the rocks, it is probable that low oxygen availability made the bottom conditions inimical to life at the time of deposition.

Slabs with a surface area in excess of 0·7 m^2 of fine grained, petroliferous marly shale were extracted from the Shore Road below, and 200 m to the west of, the Egaré Motel at Neuville. Two species of graptoloid are present – *Orthograptus quadrimucronatus micracanthus* (Ruedemann, 1947)

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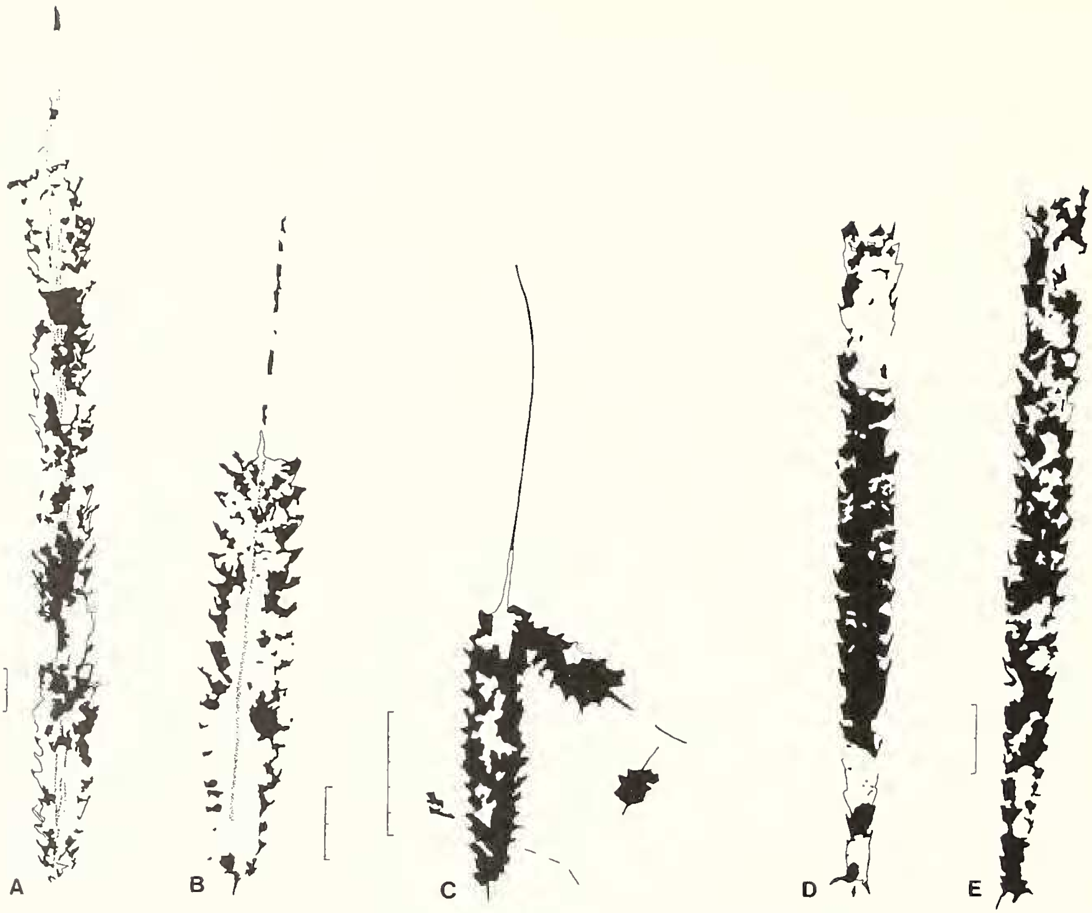


TEXT-FIG. 1. Graptoloids from Utica 3 (SM X.23262); Shore Road, Neuville, Quebec, Canada; Utica Shale, Middle Ordovician. A–C, *Orthograptus quadrimucronatus micracanthus*. D–E, *Amplexograptus praetypicalis*. Scale bars divided into mm.

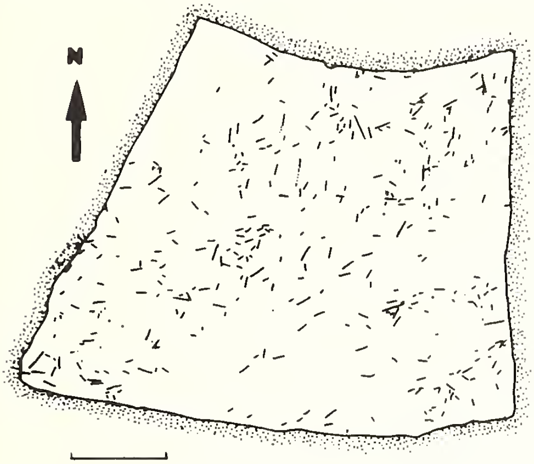
(Text-fig. 1A–C) and *Amplexograptus praetypicalis* Riva, 1987 (Text-fig. 1D–E), both in great numbers. This limited assemblage is consistent with a stratigraphical position within the *C. spiniferus* Zone, close to the base of the Utica Shale as redefined by Riva (1969).

MATERIALS

Three slabs were analysed in detail. Labelled Utica 1, Utica 2 and Utica 3, they have areas of 0·1669 m^2, 0·7700 m^2 and 0·7610 m^2 respectively and are stored in the Sedgwick Museum, Cambridge (SM X.23260–X.23262). On all three slabs the majority of graptoloids appear to be unbroken, which is rather unusual (Crowther 1978). Both sicula and nema are visible on most specimens, and relatively few graptoloids overlap one another.

The slabs were bleached with 10 per cent hydrochloric acid to lighten the matrix and improve contrast between rock and fossils. In the process, some of the periderm was removed by the violence of the reaction, leaving the outlines of the graptoloids complete but their interiors fragmented (Text-fig. 1). This does not affect identification, as the overall shape is sufficient to distinguish between the two species. Preservation was also affected by weathering; graptolites on those bedding surfaces which had been exposed were more poorly preserved than those which were freshly split.

The bleached slabs were drawn to true scale on sheets of transparent acetate. These were then photocopied and the copies used to measure lengths, widths and orientations of all complete specimens on the slabs (Text-fig. 2). Identification of the graptoloids was made at the time of drawing, which although time-consuming, ensured that each specimen could be located again if necessary. Two of the three slabs were broken during passage from Quebec to Cambridge but the drawings were put together to reconstruct the complete bedding plane. As the slabs were collected from frost-shattered and slip-rotated areas on the roadside, an arbitrary 'North' value (000°) was chosen for each slab and no correlation attempted between them.



TEXT-FIG. 2. Utica 1 (SM X.23260). Lines represent the orientation and length of graptoloids. Scale bar = 100 mm.

METHODS

Statistical techniques for testing directionality

Few studies have been carried out on the orientation of bedding plane associations of graptoloids, so that their precise behaviour in the presence of currents of varying speeds is unknown. Rickards (1975) suggested that those monograptids with hooked thecae were probably orientated differently with respect to currents than those with simple thecae. Assuming that in most species the proximal and distal ends of the colony had different properties (e.g. width and weight), it seems reasonable to assume that graptoloids generally provide directional data, rather than just orientational data. In the present study, the facing direction of the proximal end is given relative to the arbitrary 'North' (see above).

On each of the three slabs, the facing direction of the sicula and total length of a set of 100 specimens was recorded. The length of specimens was in most cases grouped into 1–5 mm, 6–10 mm, 11–15 mm and > 15 mm classes. The data were then broken down into species and length categories, and analysed statistically for evidence of preferred orientation. If a preferred direction appeared to be present, or if the sample size of a particular sub-group was too small, more colonies were chosen at random and counted until a large enough sample had been measured.

A rose diagram was plotted for each data set. The data sets were then analysed to find the mean direction and mean resultant length. It was assumed that directional data would follow a von Mises distribution, which is the circular equivalent of a normal distribution. A Rayleigh test for preferred orientation was then applied, using the null hypothesis that there is no preferred direction expressed by the data. If data are bimodal or have another form of complex distribution, then this parametric test is inappropriate and can lead to misleading conclusions (Davis 1984). To help weed out inappropriate uses of this kind, rose diagrams gave a visual check on the veracity of the results derived from the statistical technique (as suggested by Davis 1984) and thus some of the apparent results were discarded. The directional data are summarized in Table 1.

TABLE 1. Orientation and statistical likelihood of random occurrences of different sizes and species of graptoloids from Utica 1–3 (SM X.23260–X.23262).

Slab	Species	Size fraction (mm)	Sample size	$\bar{R}$	Significance (%)	Mean direction
Utica 1	*O. q. micracanthus*	All	163	0·406	1	43
		1–5	69	0·409	1	41
		6–10	63	0·326	1	53
		11–15	21	0·578	1	31
		> 15	10	0·595	2·50	45
Utica 2	*O. q. micracanthus*	All	251	0·045	Random	
		1–5	102	0·202	5	349
		6–10	48	0·267	5	340
		11–15	75	0·191	Random	
		> 15	26	0·325	10	97
	A. praetypicalis	All	91	0·176	Random	
		1–5	1			
		6–10	10	0·462	Random	
		11–15	19	0·181	Random	
		> 15	61	0·178	Random	
		[> 20	63	0·311	1	161]
	Both	All	342	0·045	Random	
Utica 3	*O. q. micracanthus*	All	223	0·192		210
		1–5	62	0·219		217
		6–10	85	0·065	Random	
		11–15	43	0·23	Random	
		> 15	33	0·456	1	209
	A. praetypicalis	All	108	0·258		212
		1–5	8	0·468	Random	
		6–10	20	0·181	Random	
		11–15	31	0·398	1	294
		> 15	49	0·364	1	34
	Both	All	331	0·069	Random	

Population and survivorship studies of graptolites

All complete specimens on the slabs were measured for use in population studies. The principal techniques used were the generation of length–frequency curves and survivorship analysis. Length–frequency distributions can show whether growth of individuals was seasonal (in which case the graph should show one or more peaks) or if growth terminated before death (in which case a peak appears at the upper size range of the population). It also gives a view of the overall population structure, but this is better seen in survivorship curves.

The use of survivorship techniques is probably best known to most palaeontologists from their application to rates of species extinction (Van Valen 1973). Several population studies on fossils have been carried out using survivorship analysis, notably on Silurian ostracodes from Gotland (Kurten 1964). In this technique, the rates at which a population is dying between consecutive ages is assessed and plotted on a semi-log scale against age. At a simple level, two extremes of survivorship curve are seen. At one end of the scale, an individual within a population has an equal chance of dying at any time, regardless of its age. This results in a straight survivorship curve, and is commonly seen where environmental stress is high and mediates mortality within the population under study. At the other end of the scale, an individual in a population may live to senility, dying from internal causes. In this case, a convex survivorship curve results and the environment is considered a minor factor in mediating lifespan, the major control being internal and metabolic (Raup and Stanley 1978).

In population biology, survivorship analysis is used with caution. Many factors affect the shape of a survivorship curve for any population. These include intrinsic factors such as potential lifespan and periodicity of reproduction, and extrinsic factors such as seasonality in the environment and population changes unrelated to birth and death – immigration and emigration to and from the area of study. Some of the classical studies of population biology have been done on islands, specifically to minimize this effect (e.g. Clutton-Brock and Ball 1987).

When the technique is applied to palaeontological data, the problems of information-loss during taphonomy serve to complicate the data much further. In any species with a soft-bodied larval stage, for example, the population preserved in the fossil record will be skewed in favour of older individuals. Current-winnowing at a later post-mortem stage can severely affect the remaining population. Bedding plane assemblages of fossils may represent gradual mortality over a period of time, or the sudden death of all of the population at once. In the first case, the population has been frozen at a series of different times, in the second it has been frozen at a single point in time (Raup and Stanley 1978). The palaeontologist can only use judgement to determine which is more likely to account for any observed fossil population.

For population studies each species on each of the Utica slabs was investigated separately. In each case length–frequency graphs were used to generate composite, age-specific survivorship curves as there was no evidence for a mass mortality event either in the graptoloids or in the sediments. Although the graptoloids were concentrated on some bedding planes, they were present throughout the rock sequence and there was no visible change in the sediment which defined graptoloid-rich beds. All populations were corrected to cohorts of 1000 before being plotted as survivorship curves (Hutchinson 1978).

To draw survivorship curves for graptoloid populations it was assumed that the length of each graptoloid was proportional to its age. In the following study, most survivorship curves are shown with the length and age of the rhabdosome on the horizontal axis. The idea that length of a graptoloid colony is proportional to its age has long been implicit. Recent studies (Rigby and Dilly in press) suggest that this assumption is justified for at least some shapes of rhabdosome, including the biserial forms studied here.

Calculating the lifespan of O. q. micracanthus *and* A. praetypicalis

Two models, both based on growth rates, for estimating the lifespan of graptoloids are available, one based on *Rhabdopleura* and one on *Cephalodiscus* (Rigby and Dilly in press); both living relatives of graptoloids which possess a skeleton.

Using the latter model, the plan area of a graptoloid colony is calculated and related to the growth rates of extant *Cephalodiscus* as measured in plan view by successive drawings of growing colonies. In experiments, this growth rate was shown to be 0·065 mm^2 per zooid per day. Using the *Rhabdopleura* model, the rate of addition of collagenous rings is used to estimate the minimum age at death of a graptoloid colony. *Rhabdopleura* zooids build their colony by the addition of such rings to 'thecal' apertures. One complete ring can be added in eight hours, and each is considered analogous to two half-rings on a graptoloid theca. The numbers of half rings required to build an average sicula and an average theca have been measured from isolated graptoloids. These suggest that about 22 days were required for the secretion of a sicula and 6·6 days for a theca. These averages take into account the variation in the number of increments that occurs within one colony and between species. These two methods of calculation can be used to give an estimate of minimum lifespan for any graptoloid.

In the case of *O. q. micracanthus*, the plan area of six specimens drawn from the Utica slabs was measured at 2 mm intervals along their lengths. The colony width changes little with distance from the proximal end, broadening quickly to its maximum value. This means that the calculated relationship between *Cephalodiscus*-based age estimates and length is effectively linear. For the *Rhabdopleura*-based age modelling, the number of thecae was measured with increasing distance from the proximal end. On average there were fourteen thecae in the first 5 mm, plus the sicula. In subsequent 5 mm intrvals there were twelve thecae. This again gives a roughly linear relationship, after the first 5 mm, between the length of the rhabdosome and the calculated age of the colony.

Amplexograptus praetypicalis specimens were measured from the Utica slabs studied here and also from drawings given by Riva (1987). It is a graptoloid species which widens gradually over the first 10–12 mm before reaching its maximum dorso-ventral width. This means that in calculating their age from *Cephalodiscus* models of colony growth, the linear relationship between length and age breaks down somewhat, because the model predicts that less time would be required to build a narrow colony than a wide one. The implications of this observation for interpretation of survivorship curves for this species are discussed below. Observations of the number of thecae per unit length for this species show that the relationship between thecal number and length is linear after the first 5 mm. Seventeen thecae plus the sicula are present in the first 5 mm, and thirteen thecae for every 5 mm thereafter. This is a close enough approximation to a linear relationship to leave unaltered any survivorship curves generated by the *Rhabdopleura* method. All survivorship curves were plotted on a single length axis, with ages calculated from the pterobranch models added, except for the data for *A. praetypicalis* where age was calculated using the *Cephalodiscus* method. In this case separate survivorship curves are drawn for *Cephalodiscus*-based age calculations.

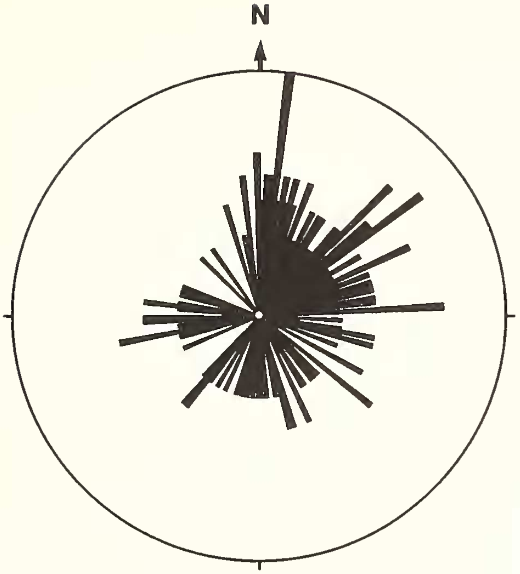
Modifications to the survivorship data

Two modifications were made to the raw survivorship information. Any part of a survivorship curve with fewer than five members of the population left was discounted. This is common practice in the analysis of human survivorship curves (Martin Bland *pers. comm.*). Any part of the curve referring to graptoloids less than three millimetres long was also discounted, for two reasons. First, very few isolated siculae are present; they may have been winnowed out, or they may have lived in geographical separation from the larger colonies (Rigby 1992). Whichever is the case, it is certain that more small graptoloids were part of the population than are recorded on this bedding plane but the amount of discrepancy is unknown. Second, the justification for using length to approximate the age of a graptoloid colony is the assumption that there is a linear relationship between the two parameters, as discussed above. Whether the growth of graptoloids was more similar to that of *Rhabdopleura* or to that of *Cephalodiscus*, the linear relationship would almost certainly have broken down in the transition from sicula to colonial graptoloid. It might be that this stage was passed as quickly as possible, to minimize the time spent in a hydrodynamically unstable form. Alternatively, it might have taken more time, because of the need to bud multiple soft-tissue clones and build several new thecae in close succession. Either way, once the assumption of a linear relationship is rejected, those individuals below true colonial size should be disregarded in an analysis of survivorship within the population.

DIRECTIONAL DATA ANALYSIS

Utica 1

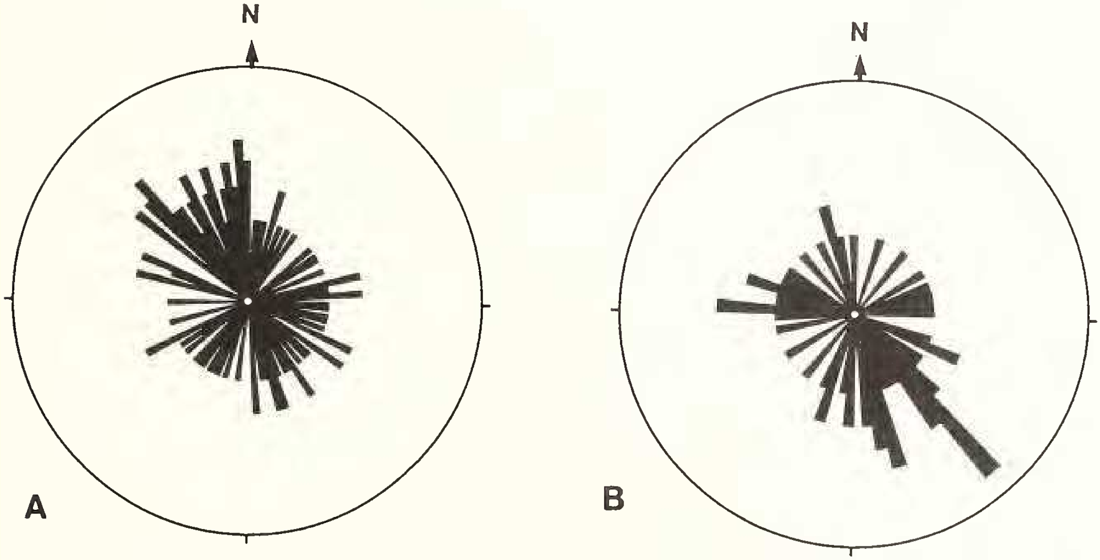
In the population overall, a preferred orientation was observed which was significant at the 1 per cent level (Text-fig. 3). All size groups showed the same result, except for the > 15 mm size division, which had a small sample size and showed a preferred orientation significant at the 2·5 per cent level. These data are consistent with orientation by a single current capable of transporting all sizes of graptoloid.



TEXT-FIG. 3. Orientation of all sizes of *Orthograptus quadrimucronatus micracanthus* on Utica 1 (SM X.23260); (n = 163; segment interval = 2°).

Utica 2

Overall, both species appeared to have a random distribution, and their size groups had random distributions, with three exceptions – the two smallest of *O. q. micracanthus* and specimens of *A. praetypicalis* more than 20 mm in length (Text-fig. 4).



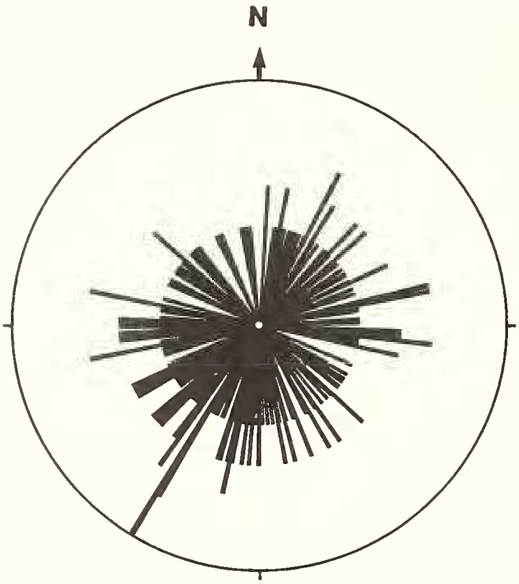
TEXT-FIG. 4. Orientation of graptoloids on Utica 2 (SM X.23261). A, small specimens of *Orthograptus quadrimucronatus micracanthus* (n = 102; segment interval = 3°). B, large specimens of *Amplexograptus praetypicalis* (n = 63; segment interval = 5°).

I think that it is not possible for a single current to have produced the observed results. As large specimens of *A. praetypicalis* are affected, but large specimens of *O. q. micracanthus* are not, it would be reasonable to assume that the specimens of *A. praetypicalis* arrived first on the seabed and were orientated before the arrival of the second species. Small specimens of *O. q. micracanthus* could have been orientated later, in a different direction, by a more gentle current of insufficient strength to affect larger colonies. Very few small specimens of *A. praetypicalis* are present.

This is a testable hypothesis, because there are places on this slab where one specimen lies on top of another. In total, thirty-three cases were found where preservation was good enough for the order of overlap to be determined. Of these, fourteen cases showed two specimens of *O. q. micracanthus* one on top of the other, seven cases showed two specimens of *A. praetypicalis* one on top of the other, ten cases showed *O. q. micracanthus* on top of *A. praetypicalis* and only two cases showed the reverse. This strongly supports the hypothesis that the two species arrived on the bedding plane at different times, with *A. praetypicalis* arriving first.

Utica 3

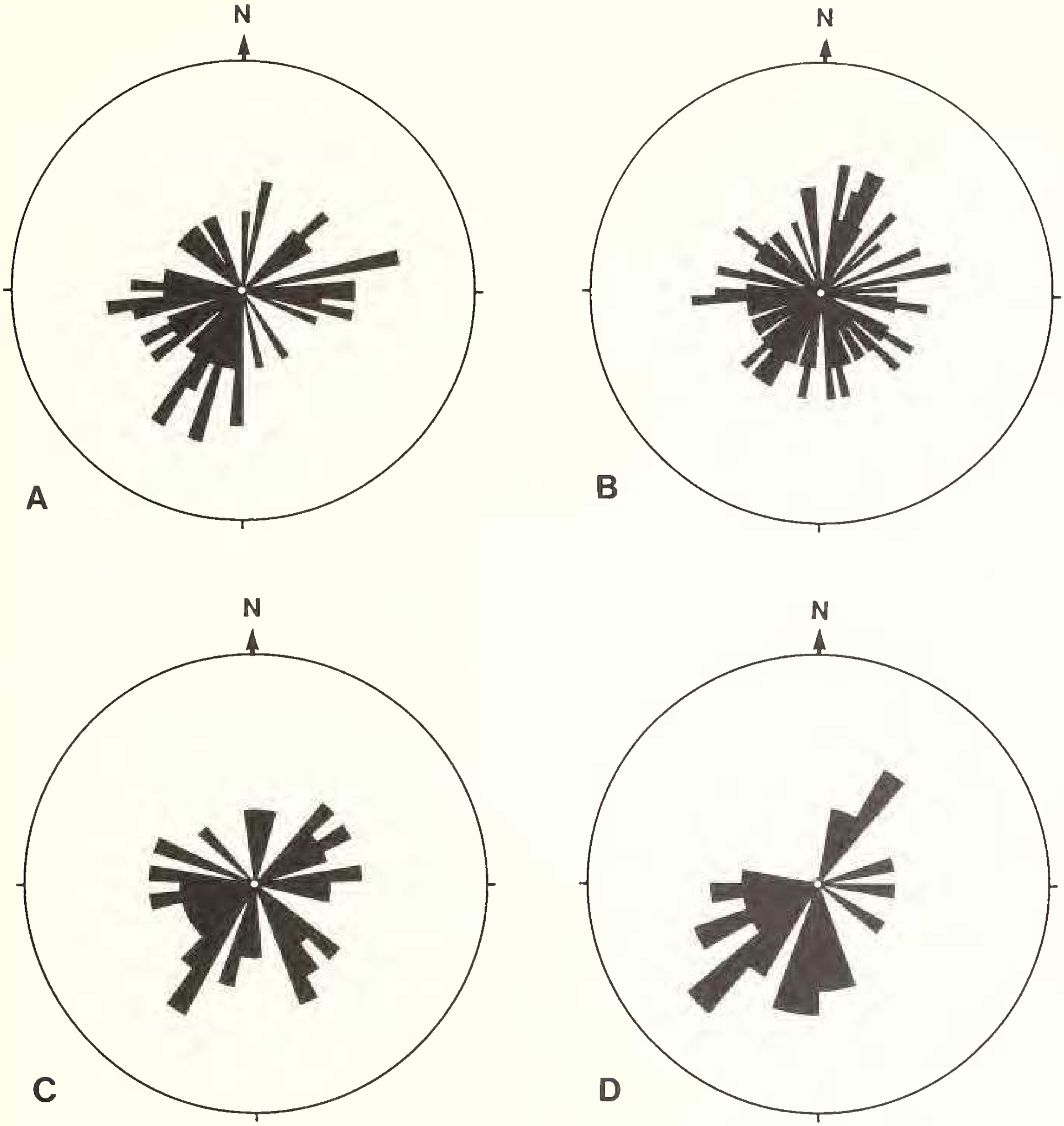
Considered together, the *O. q. micracanthus* data showed a statistically significant preferred orientation. However, cursory inspection of the rose diagram (Text-fig. 5) was enough to show that this was a function of assuming a von Mises distribution when a more complicated distribution pattern is actually shown. When the data were broken down by size, an equivocal result emerged. There was a preferred direction in specimens between 1–5 mm in length (but only significant at the 10 per cent level) and over 15 mm in length. The intermediate size ranges appeared to have a random distribution (Text-fig. 6).



TEXT-FIG. 5. Orientation of all sizes of *Orthograptus quadrimucronatus micracanthus* on Utica 3 (SM X.23262), (n = 223; segment interval = 1°).

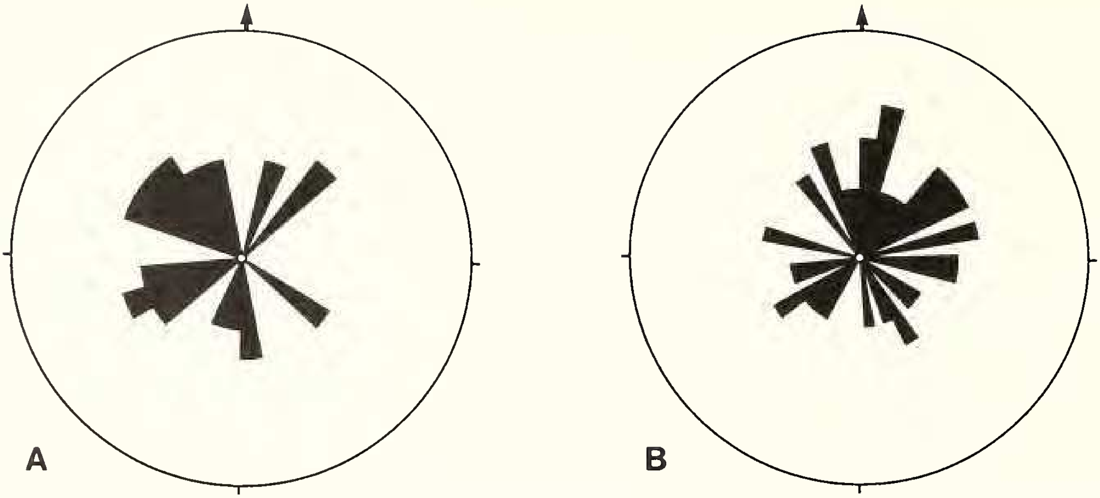
The small specimens of *A. praetypicalis* (in the 1–5 mm and 6–10 mm size ranges) showed a random distribution of direction. However, both of the larger size groups (11–15 mm and > 15 mm) showed preferred directions significant at the 1 per cent level (Text-fig. 7).

In summary, all of the larger graptoloids on this slab are orientated, but with different mean orientations. Preservation on this fragmentary slab is too poor to determine the order of arrival of



TEXT-FIG. 6. Orientation of different size-groups of specimens of *Amplexograptus praetypicalis* on Utica 3 (SM X.23262). A, 1–5 mm (n = 62; segment interval = 5°). B, 6–10 mm (n = 85; segment interval = 1°). C, 11–15 mm (n = 43; segment interval = 8°). D, > 15 mm (n = 33; segment interval = 10°).

the different species. Several currents might have been involved, but the obvious problem is that large graptoloids are orientated when small ones are not. Perhaps large and small colonies arrived at different times, which would support a seasonal growth for graptoloid colonies, possibly with annual or biannual periods of 'bloom', leading to the presence of different sizes of colony in the water column at different times of year.



TEXT-FIG. 7. Orientation of large specimens of *Amplexograptus praetypicalis* on Utica 3 (SM X.23262). A, 11–12 mm (n = 31; segment interval = 12°). B, > 15 mm (n = 49; segment interval = 8°).

POPULATION ANALYSIS

1. O. q. micracanthus

Three populations are available:

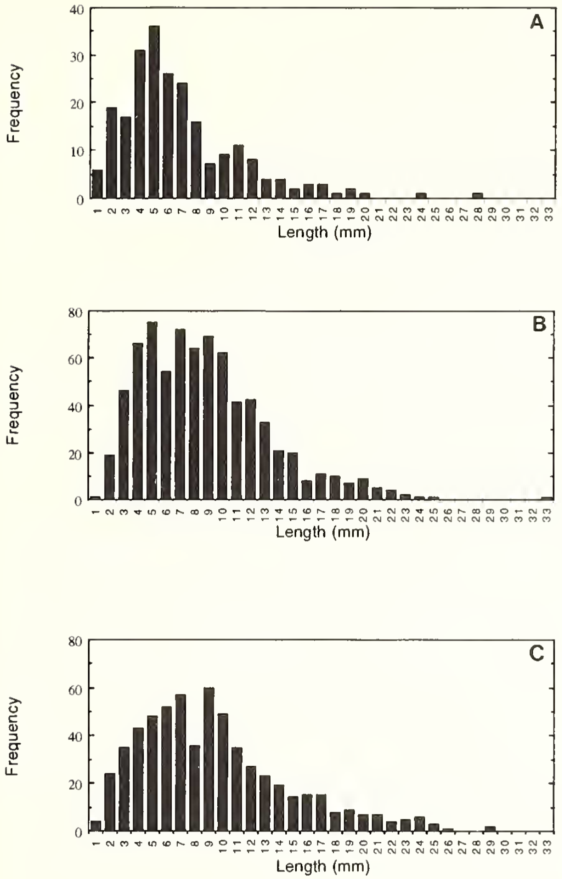
On Utica 1 (population, n = 232) the largest specimen is 28 mm long, and 5 mm is the commonest length. The length/frequency plot is a left-skewed normal distribution. (Text-fig. 8). The smooth nature of the curve suggests that growth was continuous, rather than strongly seasonal, and the absence of a terminal bulge shows that growth was continuous throughout life. These data converted into a survivorship curve (Text-fig. 9) show an initial increase in mortality rate with age followed by a long period of constant probability of death, and finally a rather irregular increase in mortality rate to the point where no individuals survive. When individuals less than 3 mm long are removed from consideration, along with those rare last specimens to survive, the remaining part of the curve is almost straight.

On Utica 2 (n = 744) a left-skewed, normal distribution of length with frequency is observed, with the commonest length of graptoloids again being 5 mm. The largest specimen is 33 mm long, which slightly exceeds the maximum length given by Elles and Wood (1901–18) for this species (Text-fig. 8). Smooth and continuous growth is suggested by the data. When the data for this slab and species are converted into a survivorship graph (Text-fig. 9), the result is distinctly convex, even with very small and very large specimens removed. With an occasional variation, the mortality rate increased continuously with length in this example.

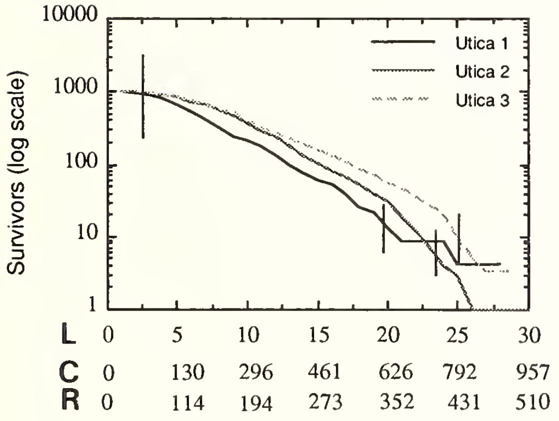
On Utica 3 (n = 609) the largest specimen is 29 mm long, and the commonest length is 9 mm. From the length–frequency graph (Text-fig. 8) it appears that continuous growth went on throughout life. When a modified survivorship curve is plotted (Text-fig. 9), the result is equivocal. Whilst definitely convex in overall form, a large segment of the survivorship curve is straight.

2. A. praetypicalis

Two populations are available. (Utica 2 and 3). Both are smaller than those of *O. q. micracanthus*, and the size-range larger.

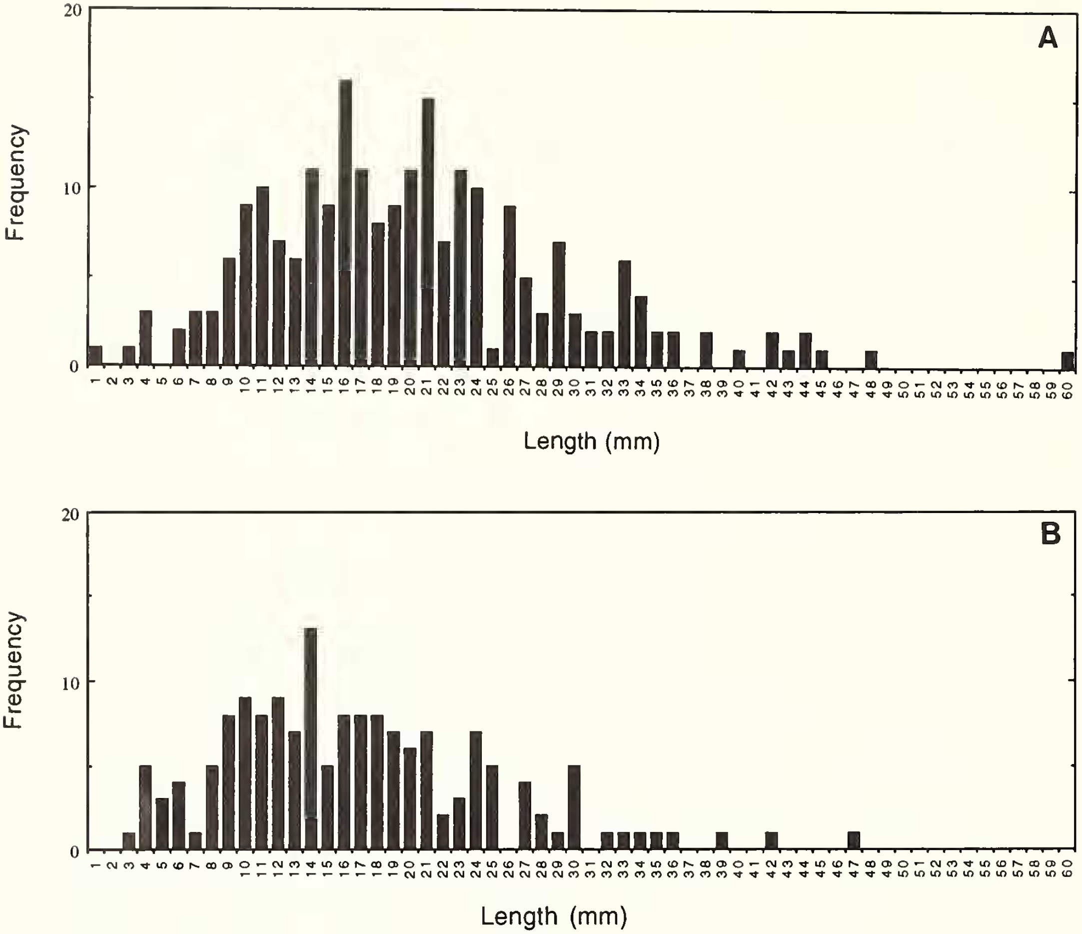


TEXT-FIG. 8. Length/frequency distributions of *Orthograptus quadrimucronatus micracanthus*. A, Utica 1 (SM X.23260). B, Utica 2 (SM X.23261). C, Utica 3 (SM X.23262).



TEXT-FIG. 9. Survivorship curves for *Orthograptus quadrimucronatus micracanthus* from Utica 1–3. L = length of specimens; C = age in days calculated from the *Cephalodiscus* model; R = age in days calculated from the *Rhabdopleura* model. Vertical bars mark the cut-off points for the data discussed in the text.

On Utica 2 (n = 266) the largest specimen is 60 mm long, and the commonest length is 16 mm. Length-frequency graphs for this species and slab are more irregular than for *O. q. micracanthus* because of the smaller sample size and greater range in length. However, the primary signal seems similar, with a left-skewed normal distribution (Text-fig. 10), indicating continuous growth through

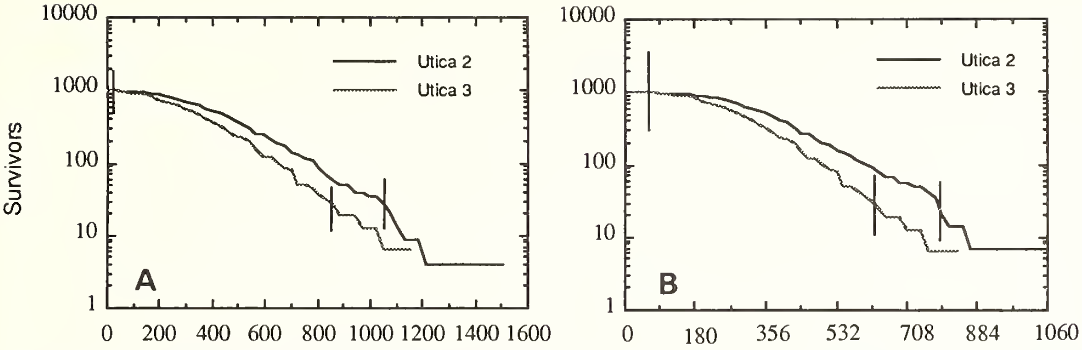


TEXT-FIG. 10. Length/frequency distributions of *Amplexograptus praetypicalis*. A, Utica 2 (SM X.23261). B, Utica 3 (SM X.23262).

life. A modified survivorship curve for these data has a convex shape (Text-fig. 11B), but with a long straight middle segment similar to the *O. q. micracanthus* curve from Utica 3.

On Utica 3 (n = 160) the largest specimen is 47 mm long and the commonest length is 14 mm. Growth appears to have been continuous (Text-fig. 10). The modified survivorship curve generated by this data (Text-fig. 11B) is clearly convex.

When age-based (rather than length-based) survivorship curves are generated using the *Cephalodiscus* model, the data points are changed because there is not a linear relationship between the age and length of this particular graptoloid for at least the first centimetre of stipe. Because the earlier growth stages are narrower, they should have taken less time to build than later growth stages, and so should represent smaller increments of time. When the graphs are corrected for this by causing the early growth stages to represent smaller periods of time, more individuals appear to have died off earlier, straightening the curve to some extent (Text-fig. 11A). The mortality rate of young specimens is increased in this method of calculation. However, for both Utica 2 and Utica 3 the overall effect is small and the curves remained noticeably convex.



TEXT-FIG. 11. Survivorship curves (calculated age in days on horizontal axis) for *Amplexograptus praetypicalis*. A, from the *Cephalodiscus* model. B, from the *Rhabdopleura* model. Vertical bars mark the cut-off points for the data discussed in the text.

DISCUSSION

Directional observations

In all three slabs there was some evidence of current orientation. The most highly orientated population is on Utica 1, where all size ranges show evidence of current sorting. The least affected slab appears to be Utica 2. On all three slabs it is possible that currents not only produced a directionality in the graptoloid population, but also a size bias due to winnowing. In the following analysis of graptoloid populations, this possibility is ignored, because the pattern of currents playing over the study area at the time of deposition was clearly complex, with several current events interspersed between the arrival of different graptoloid species (Utica 2) and possibly different sizes of the same species of graptoloid (Utica 3). The population analyses of the three slabs show strong similarities in the analysis of the same species on different slabs, and clear differences between analyses of the two species. It therefore seems likely that current winnowing had less effect than the primary controls on each species population. Having said that, it is apparent that the following study of graptoloid populations must be viewed in the light of their subsequent complex taphonomic history.

An interpretation of the graptoloid populations of the Utica Shale

Graptoloid populations from the Utica Shale produce survivorship curves that are to some extent convex. This means that mortality rate increased with age for both species present on the slabs. This could be interpreted to indicate that, in all the populations studied, inate senility was a factor in mortality. Clearly environmental stresses were also a common cause of death for members of these populations, as shown by the divergence of these curves from ideal convex shapes. The relative importance of each type of mortality varies from one slab to another. The specimens on Utica 1, which shows an almost straight survivorship curve, seem to have suffered from constantly high environmental stress, while those on Utica 2 and 3 seem generally to have experienced greater mortality with increasing age.

A large degree of environmentally-mediated mortality is to be expected in any planktonic organism, where chance water movements may remove the individual from its source of food or oxygen. Moreover, in a narrow basin such as the Taconic Ocean, it is to be expected that small changes in lateral position would have been accompanied by large changes in oceanographic parameters, as observed by Cisne and Chandlee (1982) in their 83 km transect across the basin.

It is unexpected to find any physiologically mediated overprint to this environmentally moderated mortality, because graptoloids were colonial. Colonies such as corals can live indefinitely, because they can replace dead colony members by asexual budding. Although genetic defects may eventually build up in the genome until mortality occurs, this process, if it happens at all, will take in the order of thousands of years (Jackson and Coates 1986).

An alternative interpretation of the survivorship curves is that as length increased so did the likelihood of dying-off during the next short time interval. In the populations analysed here there is evidence from the length–frequency curves for continuous growth of the graptoloid colony through life. Perhaps this suggests another explanation for the observed data. If graptoloids continued to grow throughout life, then their hydrodynamic and feeding properties, as well as their food needs, would have changed as well. For biserial forms, this change would have been a continuous increase in feeding intensity (i.e. a need for increasingly food-rich water) as the colony grew (Rigby 1992). Perhaps large individuals eventually outgrew the food availability in the water around them. In this case, environmental stresses would have operated preferentially on large colonies, and a convex survivorship curve could be generated without the need for internally controlled changes in mortality rate. This theory offers the possibility eventually of using graptoloid populations to determine oceanographic parameters like food availability and dependability for the seas in which they lived.

Synrhabdosomes

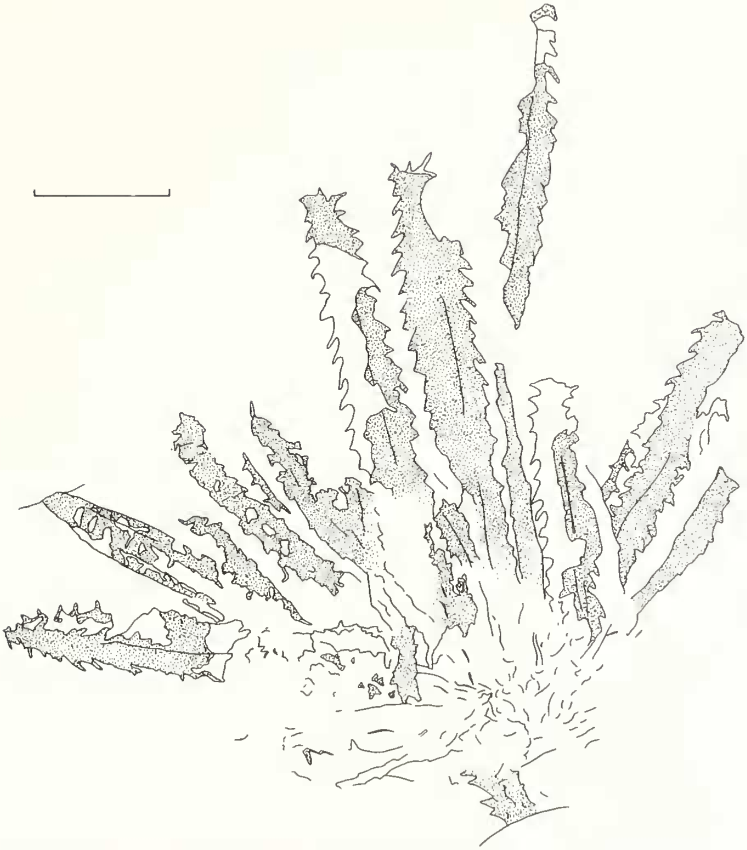
Many synrhabdosomes were found during the collection of samples from the Utica Shale. Four poorly preserved examples occur on Utica 3 (the best preserved is shown in Text-figure 12) all belonging to *O. q. micracanthus*. As in the example drawn here, they are preserved with the nemata overlapping and the sicular apertures directed outwards. This is the same orientation as those seen by Ruedemann (1947) and many other workers, and in the opposite orientation to the synrhabdosomes of *Rhaphidograptus toernquisti* described by Bjerreskov (1976). The present synrhabdosomes show a range of rhabdosome size, but no extremely large or small colonies, in contrast to those described by Ruedemann (1895, 1947) which contain graptoloids in all stages of developments, and to those of Bjerreskov (1976), in which all the constituent graptoloids are the same size.

It has been suggested that synrhabdosomes have one of two origins. They either might have been primary, serving some biological purpose, or grown by asexual budding of one colony (Kozłowski 1948; Zalasiewicz 1984). The latter would need soft part connection of colonies at an early stage and would accord well with Ruedemann's (1895, 1947) observations. Alternatively, they could be of taphonomic origin. If the first suggestion is correct the populations analysed in this paper might have been substantially different in life, especially if the formation of synrhabdosomes was common, and their duration long. If the latter suggestion is correct, perhaps many of the orientation studies conducted here give apparently random results because single graptoloid colonies were not the prime units affected by currents.

Can the occurrence of synrhabdosomes in this study suggest anything about their mode of formation? One factor that seems to be of relevance is their relative rarity. On almost 1·7 m^2 of graptoloid-rich bedding plane, only four synrhabdosomes were found (although all on the same slab). This must suggest that they were either unusual or temporary aggregates, implying that normal graptoloid reproduction was unlikely to have occurred in this way. Alternatively, they could have been common in life but disaggregated quickly after death.

On the bedding plane where the synrhabdosomes lie, some current sorting can be seen to have occurred which has affected the larger specimens of both species. Could current sorting have generated or affected the synrhabdosomes? It is hard to explain how this could have occurred. Bjerreskov (1976) observed that the synrhabdosomes she described are present in beds in which other graptoloids are strongly current orientated. This suggested to her that the synrhabdosomes had to form at a different time to the current sorting-event, most probably while the colonies were still floating high in the water column.

The solution that seems most likely to me is as follows. A major contributor to the organic content of the sea bed at the present time is marine snow. This is macroscopic aggregates of organic



TEXT-FIG. 12. Synrhabdosome of specimens of *Orthograptus quadrimucronatus micracanthus* from Utica 3 (SM X.23262). Scale bar = 5 mm.

detritus and living organisms, bonded largely by the mucus feeding-webs of zooplankton (Alldredge and Silver 1988). Marine snow collects substantial amounts of debris as it falls through the water column and brings large aggregates of organic matter to the sea bed in a single mass. Although largely composed of mucus, marine snow has considerable physical strength and will withstand high energy dissipation rates (Alldredge *et al.* 1990). Perhaps graptoloid synrhabdosomes were caught in this way. They would be uncommon, as most graptoloids would fall to rest alone, and they would be in masses too large to be affected by currents that later orientated individual colonies. The soft organic debris associated with the synrhabdosomes would have had a low preservation potential, but might have contributed to an overall increase in organic carbon within the sediment.

This interpretation must be regarded with due suspicion, as it is backed up by no firm evidence. In many ways it mirrors the suggestion (Rickards 1975) that synrhabdosomes were bound together by soft tissue. The major difference is that the soft tissue here is considered to have come from another source than the graptoloids themselves, making synrhabdosomes a taphonomic product.

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